SILICIFIED GYMNOCODIACEAN ALGAE FROM THE PERMIAN OF NANJING, CHINA

by XINAN MU *and* ROBERT RIDING

ABSTRACT. Silicification of gymnocodiacean algae in the Lower Permian at Kongshan Hill, Nanjing, China, has preferentially replaced the calcareous wall of the thallus. The original skeletal microstructure is not preserved, but acid-extraction of the silicified fossils provides information on the cortical structure and surface features of the segments and allows the gross morphology of the plants to be reconstructed. *Nanjinophycus* gen. nov., is recognized, and includes *N. ovatus* sp. nov. and *N. endoi* (Nguyen). Comparisons with Recent algae indicate that these belong to either the Rhodophyta or Chlorophyta, and the presence of sporangia-like surficial pits on the segments further support a rhodophyte-affinity. They are provisionally placed in the family Gymnocodiaceae.

南京二叠纪硅化裸海松藻类化石

穆西南　罗伯特·瑞定

摘　要

南京孔山下二叠统一些裸海松藻类的钙质壁受到选择性硅化。虽然原始骨骼的显微构造未保存下来，但用酸浸解后获得的标本却揭示了节片的皮层构造和表面特征，从而能够重塑植物体的宏观形态。本文建立了一新属－南京藻属 *Nanjinophycus* gen. nov.，它包括两个种：*N. endoi* (Nguyen) 和 *N. ovatus* sp. nov. 通过与现生藻类进行比较，表明它们可能属于红藻门，或者可能属于绿藻门。然而其节片表面所具有的孢子囊状孔穴构造证实了它们的红藻属性。暂时将之归于红藻门裸海松藻科。

STUDIES of benthic marine calcareous algae are traditionally based on thin-sections. This method has some limitations, because it is difficult to fully understand the three-dimensional morphology of the fossils in this way. Ideally thin-section examination of wall structure should be combined with study of solid specimens which can be extracted from the rock and studied in three dimensions.

In 1977 a silicified fossil horizon was found in the Lower Permian Chihsia Formation at Kongshan near Nanjing, China. This bed is rich in skeletal fossils including algae which were originally calcareous. Owing to the selective silicification, the silicified calcareous algae stand out on the weathered limestone surface. After dissolving samples, well-preserved complete segments of calcareous algae were obtained. Based on this material, together with specimens in thin-section, a new genus, *Nanjinophycus*, is recognized, represented by two species: *N. ovatus* sp. nov. and *N. endoi* (Nguyen).

After comparing these fossils with Recent algae, we consider that it is most likely that they are red algae, and we provisionally place them in the Gymnocodiaceae. These range from Permian to Tertiary. They are common in Cretaceous, and especially in Permian, shallow marine limestones of the Tethyan area and of Central and North America. It was first thought that *Gymnocodium* was a green alga (hence its name) (Pia 1920). Subsequently Pia (1937) transferred it to the red algae and Elliott established the family Gymnocodiaceae in 1955.
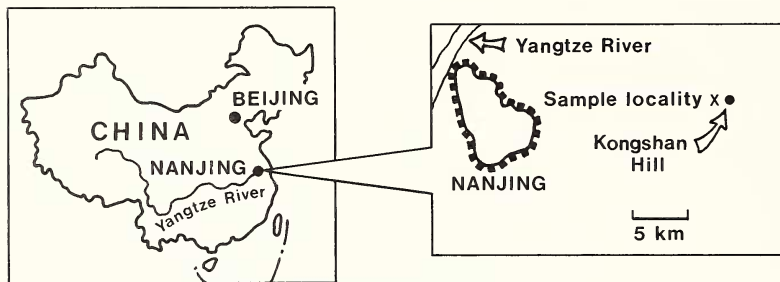
TEXT-FIG. 1. Location of Kongshan Hill, near Nanjing.

LOCALITY AND STRATIGRAPHY

A good section of the Chihsia Formation is exposed at Kongshan Hill, 20 km east of Nanjing, in eastern China (text-fig. 1). The Chihsia Formation consists of limestone with chert nodules, and siliceous shale, and is subdivided into five members in descending order (text-fig. 2):

1. Upper Siliceous Member, black thick-bedded siliceous limestone and shale (17·4 m+).
2. Chihsia Limestone Member, black to grey, medium to thick-bedded limestone with abundant chert concretions (80·9 m).
3. Lower Siliceous Member, black argillaceous chert (8·4 m).
4. Swine Limestone Member, black to grey, thick-bedded limestone with occasional chert nodules (66·7 m).
5. Clastic Member, black to grey shales with thin intercalations of greenish-grey limestone (2·3 m).

The Chihsia Formation in the Kongshan area disconformably overlies the Chuanshan Formation of late Carboniferous age. Its top is not exposed, but in the Chihsiashan area to the north-west it is overlain conformably by the Lower Permian Kuhfen Formation of Guadaloupian age.

The Chihsia Formation is rich in calcareous algae and invertebrate fossils, including fusulinids: *Misellina claudae* (Deprat), *Nankinella orbicularia* Lee, *Parafusulina multiseptata* (Schellwien); corals: *Wentzellophyllum volzi* (Yabe et Hayasaka), *Polythecalis yangtzeensis* Huang, *Hayasakaya elegantula* (Yabe et Hayasaka); brachiopods: *Linoproductus core* (Orbigny), *Orthotichia chekiangensis* Chao; ostracodes: *Bairdia chasae* Kellett, *Amphissites* Hou. Stratigraphically the Chihsia Formation corresponds to the Artinskian/Leonardian stage. Details of this succession are given in a field guide published by Nanjing Institute of Geology and Palaeontology (1979).

The material described here comes from the middle of the Chihsia Formation, 93 m above the base. Fossils directly associated with calcareous algae in this silicified bed include fusuline and smaller foraminifers, bivalves, ostracodes, echinoderms, and siliceous sponge spicules. The algae include *Nanjinophycus ovatus* (nov.), *N. endoi* (Nguyen), *Succodium* sp., *Sinoporella* sp., *Pseudovermiporella* sp., and *Tubiphytes* sp. Figured specimens are deposited in the palaeobotany collections (PB) of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.
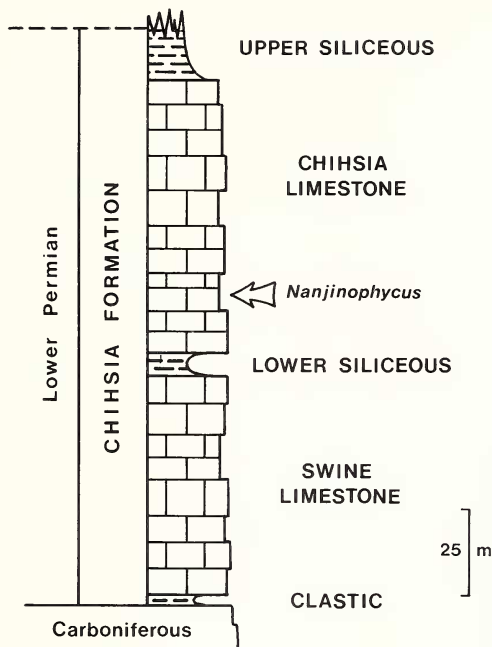
TEXT-FIG. 2. Subdivisions of the Chihsia Formation and the position of the horizon containing *Nanjinophycus*.

SYSTEMATIC PALAEONTOLOGY

Division RHODOPHYTA
?Family GYMNOCODIACEAE Elliott
Nanjinophycus gen. nov.

1970   *Succodium* Konishi; Nguyen, pp. 32–33, pl. I, figs. 6–8, 10–12; pl. IV, figs. 5–6.

Type Species. Nanjinophycus ovatus sp. nov.

Derivation of name. Nanjin from Nanjing, the new rendering of Nanking, capital of Jiangsu Province, China. Phycus from Greek phykos seaweed.

Generic diagnosis. Thallus erect; branched or, unbranched (?); segmented. Segments cylindrical, club-shaped, ovoid, or spherical. The central part of the segment is composed of longitudinally arranged medullary filaments which branch to produce divergent cortical filaments curving towards the exterior surface. The distal parts of the cortical filaments expand to form ovoid or nearly spherical vesicles, connected to the surface by at least two, probably four, terminal branchlets (text-fig. 3). The short branchlets expand exteriorly and have circular cross-sections. Thus, the cortex is divided into a

thick inner part with curved filaments and vesicles, and a thin outer part with terminal branchlets. The vesicles are mutually juxtaposed and in plan view form a polygonal network.

Cavities, believed to be concerned with reproduction (sporangia or gametangia), occur within the cortex, opening directly on to the surface to form broad hollows (here termed 'sporangia' to conform with general usage in other papers on similar fossil algae). Calcification largely confined to the cortex, but the medulla is also occasionally calcified, perhaps secondarily.
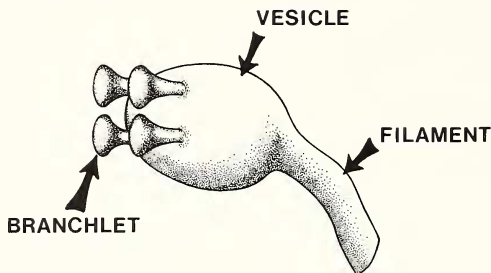

TEXT-FIG. 3. Reconstruction of the distal part of cortical filament in *Nanjinophycus ovatus* showing ovoid vesicle and four terminal branchlets.

Remarks. Nguyen (1970, p. 32) described specimens, from loose pebbles of Permian limestone at Campha Harbour in northern Viet Nam, which she regarded as belonging to *Succodium*. She recognized, however, that they 'present some previously unknown characteristics in the outermost cortical layer. In these specimens, each utricle swelled up into ball-like expansions, then forked in developing two ultimate and minute cup-shaped vesicles.' She assumed that this production of branchlets from the utricles 'has not been well-preserved in the original specimens' (Nguyen 1970, p. 32).

We believe that the material figured by Konishi (1954) is sufficiently well preserved to demonstrate that the vesicles of *Succodium* do not branch (see Discussion below). In addition, specimens of *Succodium* which occur in the material from Kongshan described here, confirm this interpretation. Consequently, we here place *S. endoi*, described by Nguyen, in *Nanjinophycus*.

EXPLANATION OF PLATE 36

Figs 1-6. *Nanjinophycus ovatus* gen. et sp. nov., Lower Permian Chihsia Limestone, Kongshan Hill, Nanjing. Scanning electron photomicrographs. 1, complete segment showing ovoid shape and surface pits interpreted as reproductive organs (PB 68036, holotype), ×20. 2, as 1, top view of specimen showing terminal opening (PB 68036, holotype) ×17. 3, broken specimen showing peripheral row of holes formed by the cortical vesicles (PB 68037, paratype), ×18. 4, as 1, showing partial spalling of the outer part of the cortex revealing the vesicles just below the surface. Spalling occurs where the cortex is weakened at the plane of greatest width of the vesicles (PB 68036, holotype), ×45. 5, side view of vesicles showing their ovoid shape. Vesicle on right shows the cortical filament entering at its base. Terminal branchlets are not visible (PB 68038, paratype), ×185. 6, side view of outer part of cortex showing lower parts of vesicles, connected below with cortical filaments (middle of figure) and upper parts of vesicles with terminal branchlets (top of figure, not in focus). At extreme top right a terminal branchlet (arrowed) is seen clearly extending upwards from a vesicle. Spalling of the surface of the skeleton has occurred, as in fig. 4 (PB 68039, paratype), ×185.

PLATE 36

MU and RIDING *Nanjinophycus ovatus*
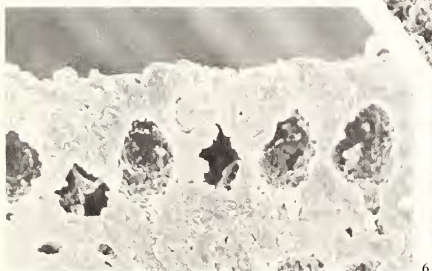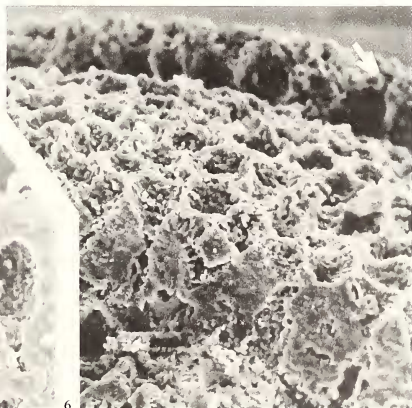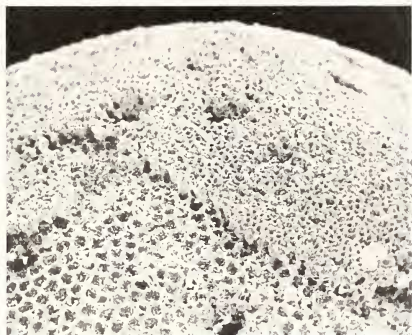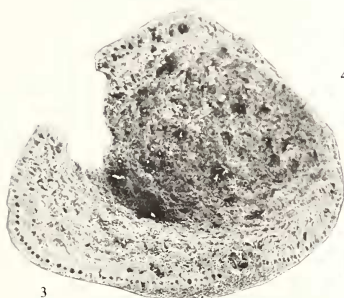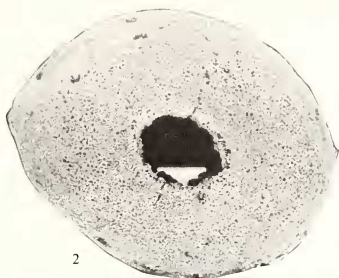
Nanjinophycus ovatus sp. nov.

Plate 36, figs. 1–6

Types. Holotype, PB 68036; paratypes, PB 68037, PB 68038, PB 68039. All solid (unsectioned) specimens on SEM stubs.

Material. Eight complete segments and one segment in thin section.

Diagnosis. *Nanjinophycus* with large ovoid, pear-shaped or spherical segments.

Description. Segments up to 5·6 mm long and 4·0 mm or more in diameter. Circular openings 0·49–0·87 mm in diameter occur at both ends of the segments. Outer cortex up to 0·058 mm thick, inner cortex thickness not determined. Vesicles spherical or ovoid, in the latter case narrowing exteriorly up to 0·080 mm in diameter. Terminations of branchlets at the surface of the segment are 0·010–0·029 mm in diameter (Table 1).

TABLE 1. Dimensions of *Nanjinophycus ovatus* from Kongshan Hill, Nanjing. L, segment length; D, segment external diameter; Pc1, vesicle diameter; Pc2, diameter of external opening of terminal branchlet; Sp, 'sporangium' diameter.

Specimen	L (mm)	D (mm)	Pc1 (μm)	Pc2 (μm)	Sp (μm)
PB 68036 (holotype)	4·6	3·7	40–80	10–20	150–180
PB 68037 (paratype)	3·5	2·7	35–47	12–23	210
PB 68038 (paratype)	> 5·6	4·0	55–66		
1	4·9	3·5	35–58	18–23	
2	2·2	2·2	41	23	
3	> 2·1	2·2	35–58	23	
4	2·8	2·8	41–58	23	
5	4·1	3·1	41–58		
6	∼2·5		47–58	17–29	

Remarks. *N. ovatus* is distinguished from *N. endoi* by having larger, rounded segments. Because the fossil has so far only been studied from isolated segments we do not know the nature or occurrence of branching.

Occurrence. Lower Permian, Chihsia Formation, Jiangsu Province, China.

Nanjinophycus endoi (Nguyen)

Plate 37 figs. 1–6

1970   *Succodium endoi* Nguyen, pp. 32–33, pl. I, figs. 6–8, 10–12; pl. IV, figs. 5–6.

Material. Many complete segments and fragments of segments with numerous specimens in thin section.

EXPLANATION OF PLATE 37

Figs. 1–6. *Nanjinophycus endoi* (Nguyen), Lower Permian Chihsia Limestone, Kongshan Hill, Nanjing. 1–5 are scanning electron photomicrographs, 6 is thin section photomicrograph. 1, complete segment showing cylindrical form and surface pits interpreted to be reproductive organs (PB 68040), × 17. 2, as 1, oblique view of surface, specimen is broken revealing vesicles in outer part of cortex (PB 68040), × 41. 3, detail of 2, showing layer of vesicles just below surface, smooth surface in lower part of photograph is glue (PB 68040), × 160. 4, complete segment showing terminal opening, the fine pores on the surface are the openings of the terminal branchlets arising from vesicles below the surface (PB 68041), × 42. 5, complete segment, partially broken at end revealing internal structure. Four pits, interpreted as reproductive organs, are visible on the surface (PB 68042), × 20. 6, oblique section of segment showing outer cortical zone with vesicles and inner medulla with traces of filaments preserved by bituminous material (PB 68043), × 60.
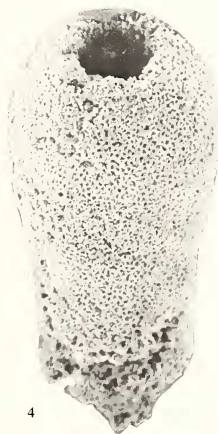
PLATE 37
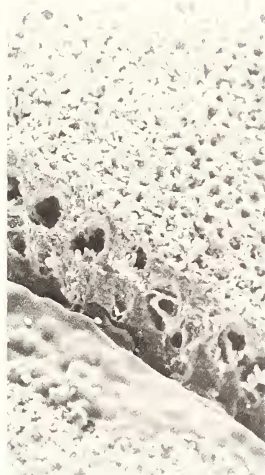
MU and RIDING, *Nanjinophycus endoi*

Diagnosis. Small *Nanjinophycus* with cylindrical or club-shaped segments.

Description. Thallus dichotomously branched. Cylindrical segments commonly constricted in the middle, with the diameter of the upper part larger than that of the lower part; ends rounded. Segments 1·17 to 4·68 mm long and 0·22–1·74 mm in diameter. Circular openings, 0·35–0·52 mm in diameter, occur at the upper and lower ends. Cortex up to 0·46 mm thick, outer cortex up to 0·077 mm. Vesicles elliptical or ovoid, narrowing exteriorly, usually 0·035–0·058 mm in diameter. Terminations of branchlets at the surface of the segment are up to 0·011–0·029 mm in diameter. The opening of the sporangia on the surface is 0·120–0·2 mm in diameter (Table 2).

TABLE 2. Dimensions of *Nanjinophycus endoi* from Kongshan Hill, Nanjing. Abbreviations as for Table 1; Pm, diameter of medullary filament.

| Specimen	L (mm)	D (mm)	Pm (μm)	Pc1 (μm)	Pc2 (μm)	Sp (μm)
1	4·7	1·5	39–45	13–29	10–20	130–210
2	3·6	1·5	35–41	12–23	12–23	140–200
3	2·0	0·9	39–44	11	18–23	
4	1·6	1·0	37–47	17–23	23	
5	1·9	0·9	35–58	17–20	23	
6	2·4	1·0	41–58	23	18–23	81–120
7		1·6	43–57	11–29		
8	3·3	1·7	47–70	17–29	17–29	

Remarks. This species differs from *ovatus* in having an elongate segment and being generally smaller in size. The material described by Nguyen (1970) is comparable with that from Kongshan in the shape of the segments and morphology of the vesicles. It is also similar in vesicle size, but in segment size it occurs within the lower range of that for the Kongshan material: Nguyen (1970, p. 33) reports a segment length of 1·03 mm and segment diameters of 0·26–0·67 mm, which compare with dimensions of 1·17–4·68 (length) and 0·22–1·90 mm (diameter) for this species from Kongshan (text-fig. 4). Consequently, the vesicle size of the Campha Harbour specimens is large relative to segment size, when compared with the Kongshan material. Another difference is the absence of conceptacle-like structures in the Campha Harbour material. This may be apparent rather than real because Nguyen examined the material in thin section and we have only observed conceptacles in solid silicified specimens etched from the matrix. Therefore, some differences exist between the material from these two localities but we consider them to be insufficient to separate the specimens on taxonomic grounds.

Occurrence. Lower Permian, Chihsia Formation, Jiangsu Province, China. Loose pebbles possibly from ?Permian, ?Campha Harbour Formation, Campha Harbour, northern Viet Nam (Nguyen 1970, pp. 2 and 33).

DISCUSSION

The shape of the segments and the internal structure of *Nanjinophycus* are similar to those of *Succodium* Konishi, the cortex of which is also subdivided into inner and outer parts. There are two main differences between these genera:

(a) The vesicles of *Succodium* (called gametangia by Konishi 1954) are not branched, but taper into thin filaments distally; this tapered part making the outer cortex. This is clearly shown in Konishi's (1954, fig. 1) reconstruction of *S. multipilularum* and is supported by our examination of *Succodium* from Konshan and also by Korde's (1965, figs. 51 and 52) description of the genus. In *Nanjinophycus* the vesicles divide distally into several terminal branchlets (text-fig. 3). The exact number of terminal branchlets present in *Nanjinophycus* is uncertain. In thin section at least two branchlets can be seen (Pl. 37, fig. 6), but SEM examination of the surface of the cortex (Pl. 36, fig. 4; Pl. 37, fig. 3) shows several branchlet
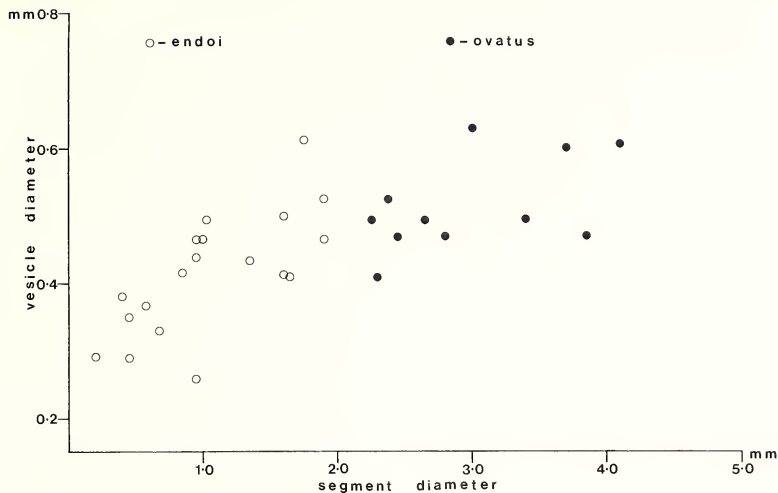
TEXT-FIG. 4. Vesicle and segment dimensions of *Nanjinophycus endoi* (open circles) and *Nanjinophycus ovatus* (black circles) from Kongshan Hill, Nanjing. Position of circle indicates mean value of vesicle size.
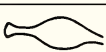
openings relative to each underlying vesicle. By comparing vesicle size with branchlet openings we estimate that there are probably four branchlets in both *N. ovatus* and *N. endoi* (text-fig. 3), although the number could range from two to five.

(b) In *Succodium* no conceptacle-like structures have been reported in the type species, but Korde found a new species, *S. difficile*, with large ovoid structures deep within the cortex (Korde 1965, pl. 55, fig. 3a, b). She regarded these as sporangia although the photographs do not represent conclusive evidence for this. In *Nanjinophycus* from Kongshan sporangia-like structures are conspicuous on the surface of some segments (Pl. 36, fig. 1; Pl. 37, fig. 1). We do not regard the apparent absence of sporangia in the Campha Harbour specimens as a serious obstacle to placing them in *Nanjinophycus*. The principal feature in thin section which distinguishes the genus is the shape of the vesicle and presence of branchlets. 'Sporangia' are, however, significant for assessing the systematic position of the alga.

The structure of the cortex of *Nanjinophycus* is similar to that of the phylloid alga *Eugonophyllum* Konishi and Wray which is subdivided into inner and outer cortex. In *Eugonophyllum* the inner part of the cortex is composed of ovoid utricles which give rise to branchlets in the outer part. There are also sporangia-like structures in *Eugonophyllum*. The principal differences between these two genera are that *Eugonophyllum* has a leaf-like thallus while *Nanjinophycus* is cylindrical and segmented, and the sporangia-like structures in *Eugonophyllum* usually form protuberances on the surface (Konishi and Wray 1961, pl. 75, figs. 6, 8–13, 16, 17) whereas they do not in *Nanjinophycus*. *Nanjinophycus* is also similar to *Gymnocodium* Pia and *Permocalculus* Elliott in thallus shape and internal structure, but the cortex of *Gymnocodium* and *Permocalculus* lacks vesicles.

Nanjinophycus is one of a number of genera (*Gymnocodium, Permocalculus, Succodium, Eugonophyllum*), common in parts of the Carboniferous and Permian, which show several similarities

in their organization (text-fig. 5). Of these, *Nanjinophycus*, *Gymnocodium*, *Permocalculus*, and *Succodium* form a coherent group which shares a branched, segmented structure and which, with the exception of *Succodium*, definitely have reproductive organs. They are distinguished principally on the structure of the cortical filaments: those of *Succodium* having a vesicle but being unbranched, those of *Gymnocodium* and *Permocalculus* having no vesicle but dividing into two or more branchlets, while *Nanjinophycus* is characterized by a distinctive vesicle giving rise to several terminal branchlets.

	SEGMENT/THALLUS	REPRODUCTIVE ORGANS	CORTEX (in thin section)
Nanjinophycus	ovoid cylindrical or spherical segments	internal, opening on surface	
Gymnocodium			
Permocalculus			
Succodium		?	
Eugonophyllum	phylloid thallus	make protuberances on surface	

TEXT-FIG. 5. Morphological features of *Nanjinophycus* and comparable Upper Palaeozoic genera.

If the existence of reproductive organs reported by Korde (1965) in *Succodium* can be substantiated, then we would agree with her that this too belongs with the Gymnocodiaceae, which would then comprise *Gymnocodium*, *Nanjinophycus*, *Permocalculus*, and *Succodium*. The existence of reproductive organs is an important factor in such an assignment because otherwise the vegetative morphology alone of these genera is also consistent with them being codiaceans (Riding 1977, p. 207). The differences between *Nanjinophycus* and these other genera (presence of vesicle plus branchlets in the cortical filaments of *Nanjinophycus*) are sufficient to warrant *Nanjinophycus* being accorded generic status, it would not be appropriate to regard this material as representing new species of either of the other three genera.

Affinities

There are a few living algae which are comparable to some extent with *Nanjinophycus*, although none of them is exactly analogous with it. Members of the Chaetangiaceae (Rhodophyta), especially *Galaxaura* Lamouroux, are most similar to *Nanjinophycus*. *Galaxaura* is an erect, calcified alga consisting of cylindrical segments. Internally it has a multiaxial structure formed by outwardly curved filaments which arise from the medulla. Some of its asexual forms have one layer of large cortical cells, which produce stalk cells followed by terminal cells (Chou 1945, pl. 3, figs. 2 and 4) (text-fig. 6). This anatomical structure is very similar to that in *Nanjinophycus*. It is possible that the vesicle in *Nanjinophycus* corresponds to the cortical cell in *Galaxaura* and that the terminal branchlet corresponds to both the stalk and terminal cells. In the sexual forms of *Galaxaura* the male and female reproductive organs develop within the thallus below the surface (text-fig. 7). They are globose in form and connect to the exterior by an orifice. The female conceptacle is usually larger than the male conceptacle. When the conceptacle is mature the sexual cells are released, enlarging the orifice. The resulting depression in the surface of the thallus is very similar to the hollows on *Nanjinophycus*;
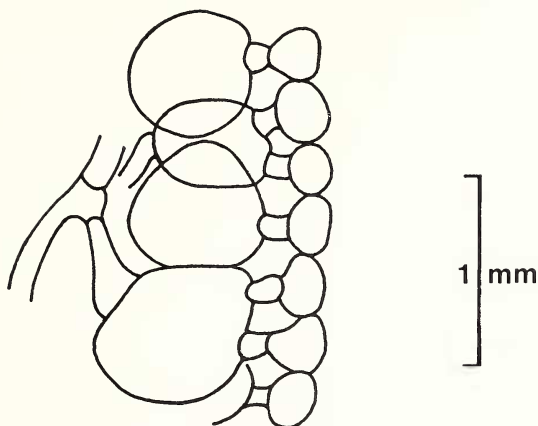
TEXT-FIG. 6. *Galaxaura*, detail of cortical cells (from Svedelius 1945, fig. 20*b*).
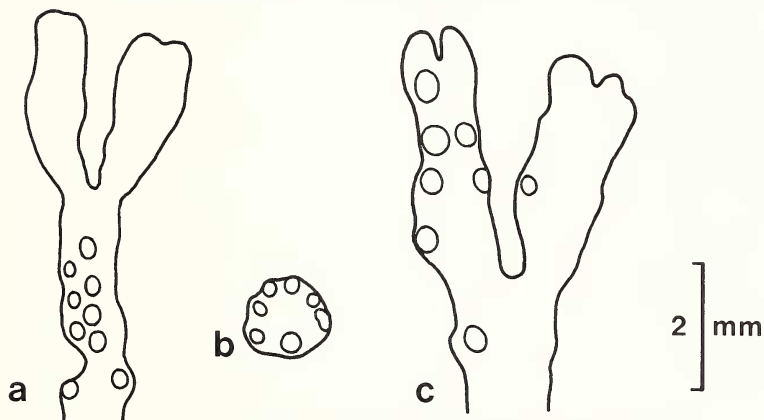
TEXT-FIG. 7. *Galaxaura*, conceptacles (from Svedelius 1945, fig. 11*a–c*). *a*, *c*, female; *b*, male.

we interpret the latter as conceptacles. But it is difficult to say whether they are male or female. In some *Galaxaura* species the conceptacles are concentrated on certain segments of the thallus, usually on those of the terminal parts of the plant. This may explain why only a few of our specimens of *Nanjinophycus* segments bear conceptacles. The cortex of *Galaxaura* is calcified and this preserves the fine reticular network of the surface cells. A similar pattern is seen in *Nanjinophycus*.

Nanjinophycus also resembles some members of the Codiaceae, both in the thallus morphology and
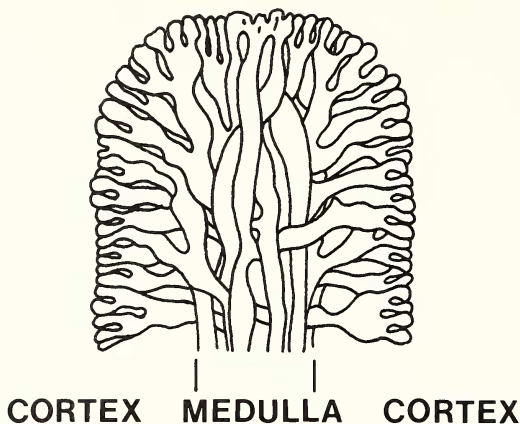
TEXT-FIG. 8. Longitudinal section through part of a *Halimeda* segment showing internal filamentous structure (from Hillis-Colinvaux 1980, fig. 6).
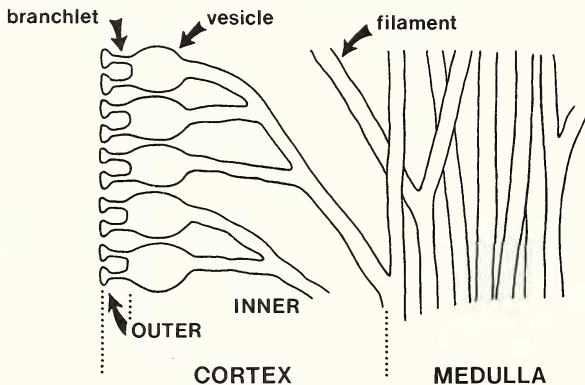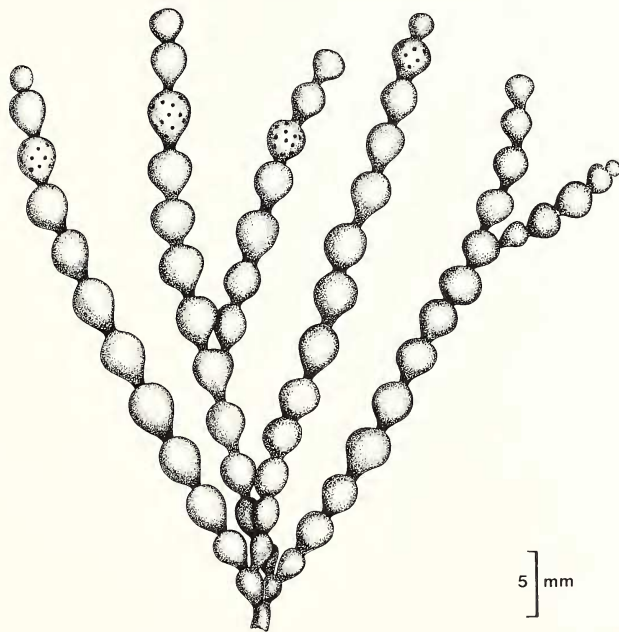

TEXT-FIG. 9. Vegetative construction of *Nanjinophycus*, showing a section of part of a segment from the centre (right) to exterior surface (left).

in internal structure, notably *Halimeda* Lamouroux. *Halimeda* is segmented and calcified. The internal structure is composed of tubular filaments without cross partitions (siphoneous organization), which are differentiated into medulla and cortex (text-fig. 8). The latter is composed of side branches (utricles) which may branch again several times to divide the cortex into a series of layers. Each secondary utricle usually gives rise to 2–4 peripheral (outer) utricles. *Nanjinophycus* also shows differentiation into medulla and cortex (text-fig. 9). The outer cortex of *Nanjinophycus* could, by
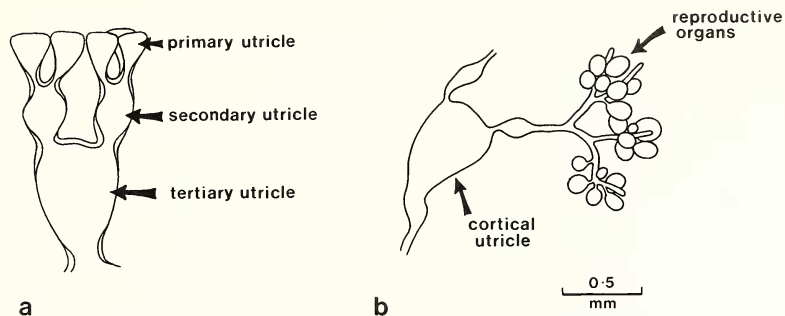
TEXT-FIG. 10. (a) *Halimeda*, utricles in the cortex (from Hillis-Colinvaux 1980, fig. 7). (b) *Halimeda* gametangia forming clusters on filamentous extensions of the cortical utricle (from Egerod 1952, fig. 19c).
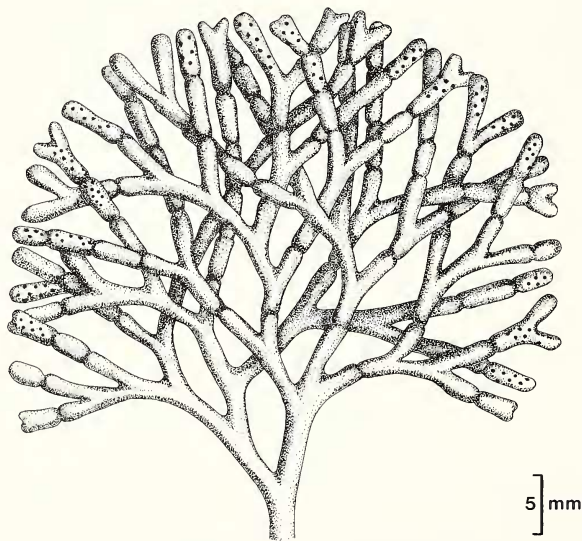

TEXT-FIG. 11. Reconstruction of *Nanjinophycus ovatus*.

analogy, correspond with the peripheral layer of utricles in *Halimeda*. The vesicles in *Nanjinophycus* would then correspond to the secondary utricles of *Halimeda* (text-fig. 10*a*). However, the secondary utricles in *Halimeda* are not usually so obviously swollen as the ovoid to spherical vesicles seen in *Nanjinophycus*. Despite this difference of detail, the general structural pattern is the same. The principal difference between *Nanjinophycus* and *Halimeda* lies in the position and shape of the reproductive organs. In *Halimeda* the gametangia are grape-like clusters on stalks which rise above the surface of the thallus (text-fig. 10*b*). This is quite different from the sporangia-like structure on the surface of *Nanjinophycus*. There is also some difference in the degree of calcification between *Halimeda* and *Nanjinophycus*. In *Halimeda* calcification usually extends into the medulla, but in *Nanjinophycus* it is mainly limited to the cortex (see below).

From the previous comparisons we can see that there are at least two possible interpretations of the affinities of *Nanjinophycus*; either a red algal affinity, in comparison with *Galaxaura*, or a green algal affinity, comparable with that of *Halimeda*. The principal difficulty for a green algal affinity of *Nanjinophycus* is the absence of large conceptacle-like structures in Recent Codiaceae, but we cannot exclude the possibility that *Nanjinophycus* is a green alga. Nevertheless, on the basis of both vegetative structure and organs believed to be reproductive, together with the pattern of calcification, it seems most likely that *Nanjinophycus* is a red alga similar to Recent Chaetangiaceae. In reconstructing the overall form of the thallus of *Nanjinophycus* (text-figs. 11, 12) we have used this analogy with *Galaxaura*.

The fundamental reason for the uncertainty regarding the affinity of *Nanjinophycus* is related to the fact that abundant parallelism results in the similarities of general internal structural patterns among algae with different affinities and the algal skeletons alone fail to reveal the critical criteria to distinguish between them. The mode of calcification in *Nanjinophycus* is similar to that shown by

5 mm

TEXT-FIG. 12. Reconstruction of *Nanjinophycus endoi*.

Galaxaura and *Halimeda*: the $CaCO_3$ is deposited on the surfaces of the cells and in the spaces between the filaments. When the plant dies the soft parts will decay rapidly—first, the cell content and then the cell wall. Only the calcareous skeletons can normally be preserved as fossils. Within this type of calcareous skeleton only the outlines or moulds of the soft parts of the algae are preserved, including both the vegetative and reproductive structures. In these circumstances it is not possible to know the detail of the cell structure—for example, the presence or absence of cross-walls within the filaments, and the development of reproductive organs, not to mention the pigments and food storage organs within the cells. All these features are very important for identification of the systematic position of the alga. Furthermore, even the outer mould does not preserve those parts of the thallus which were not calcified. All this compounds the problem of making anatomical comparisons, as well as more detailed ones, between fossil and Recent algae. Thus, we do not know in this particular material, nor in *Succodium* and other members of this general group, if there are cross-partitions within the filaments. If they did occur we could more confidently assign these specimens to the red algae. If they did not then they are more likely to be green algae (text-fig. 13). Although we tentatively place *Nanjinophycus* in the red algae, a lot of questions remain. For example, we do not know how the cells make up the terminal branchlet in *Nanjinophycus*, nor the external shape of the terminal cell, flat or curved. We do not know if there were any assimilatory filaments on the surface of the terminal cell, nor whether the reproductive organs were male or female. Without more detail about anatomical structure of the alga any assignment of affinity is not conclusive. In order to learn more we must search for specimens in which the soft parts are preserved. These could occur where silicification occurred very early.

In most of the material we have examined, the cortex is completely silicified and it is not possible to recognize a primary discontinuity in the internal structure of the fossil which could reflect the original limit of calcification. However, one specimen of *N. endoi* in thin section shows only partial silicification and the cortex appears as a distinct zone of brownish sparite juxtaposed against the interior clear sparite of the medullary region (Pl. 37, fig. 6). The medulla also clearly shows the traces of filaments. In Recent *Galaxaura* calcification is normally restricted to the cortex and although it varies in degree and location it is relatively constant for each species (Svedelius 1945, 1953). It is
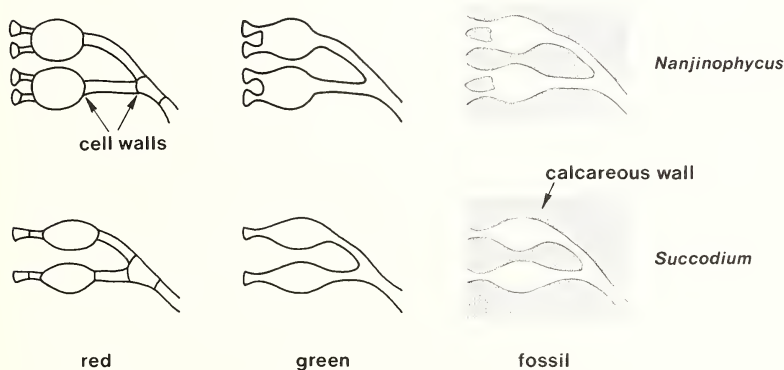
TEXT-FIG. 13. Comparison between possible original organization of cortical filaments in *Nanjinophycus* and *Succodium* and the resulting fossil morphology. If cross-partitions occur but are not calcified the final appearance will be similar to specimens lacking original cross-partitions; yet this feature, if preserved, could help to distinguish between a red and green algal affinity.

therefore likely that the brown sparite cortical zone of *N. endoi* represents the original zone of calcification, and that it was similar in all specimens of this species. In *Galaxaura*, however, the medullary filaments are not usually calcified, although their preservation in *N. endoi* suggests that they had a veneer of carbonate sufficient to preserve their shape and position until the cement filling the interior of the segment was precipitated.

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